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# Potential influence of nutrient availability along a hillslope: Peatland gradient on aspen recovery following fire

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The Boreal Plains (BP) of Western Canada have been exposed to increasing disturbance by wild-fire and host a mixture of upland-wetland-pond complexes with substantial quantities of trembling aspen (*Populus tremuloides* Michx.) throughout the terrestrial areas. The ability of these tree species to regenerate within both upland and wetland areas of the BP following wildfire is unclear. The purpose of this study was to investigate the influence of fire on nutrient dynamics in soil and water in peatlands and forested landscapes in the BP and relate this to aspen regeneration. Nutrient concentrations, nutrient supply rates, and net nutrient mineralization rates were determined in burned and unburned sections of a peatland and forest and compared with the regeneration of aspen. $NO_3^-$, $NH_4^+$, and P varied spatially throughout the landscape, and differences were observed between peatland and upland areas. In general, differences in nutrient dynamics were not observed between burned and unburned areas, with the exception of P. Nutrient and growth data suggest that aspen do not require nutrient-rich conditions for regeneration and instead relied on forest litter to satisfy nutrient demands. Although the peatlands contained high nutrients, aspen did not flourish in the combination of anoxic and aerobic organic-rich soils present in this area. Although aspen may use peat water and nutrients through their rooting zones, peatlands are unsuitable for aspen re-establishment in the long-term. However, the combination of abundant nutrients in surface mineral soils in peat margins may indicate the vulnerability of margins to upland transformations in later successional stages.

## 1 IN T RO D U CT I O N

The Boreal Plains (BP) region of Western Canada covers approximately 650,000 $km^2$ and contains a mixture of forested land and pond- peatland complexes. The BP have been highly subjected to natural and anthropogenic disturbances, including mining, harvesting, oil exploration, and fire (Rooney, Bayley, & Schindler, 2012). Subhumid conditions, where potential evapotranspiration often exceeds precipi-tation (P) in the BP (Brown, Petrone, Mendoza, & Devito, 2010; Devito, Creed, Gan, et al., 2005), make this ecozone susceptible to wildfires (Fauria & Johnson, 2008; Flannigan, Logan, Amiro, Skinner, Stocks, 2005; Weber & Stocks, 1998). Although fires are needed to maintain system heterogeneity through the destruction of current stands, the periodic occurrence of fires has other ecological consequences (Weber & Stocks, 1998). Trembling aspen (*Populus Temuloides* Michx.), the dominant upland species in the BP, often rapidly regenerate following disturbance due to resource reserves in the expansive rooting systems of the tree (Calder, Horn, & St. Clair, 2011; DesRochers & Lieffers, 2001; Schier & Campbell, 1978; Schier, Jones, Winokur, 1985). During disturbances, such as cutting, harvesting, and fire, the hormone auxin can be destroyed where its release can be inhibited from the main stem (Fraser, Lieffers, & Landhäusser, 2004; Schier et al., 1985; Schier & Campbell, 1978), which acts to not limit sucker growth. Further, in the event of fire, increased temper-atures allow for the production of cytokinins in root meristems, thus enhancing root and sucker growth (Bartos & Meuggler, 1981; Romme et al., 1997; Schier et al., 1985). Although this is well-observed in forested sites, aspen regeneration is nearly absent in peatlands (Beckingham & Archibald, 1996). The controls on aspen regeneration may be hydrological and/or biogeochemical in nature (Buck & St. Clair, 2012; Hemming & Lindroth, 1999) and have implications for when and where the aspen may successfully regenerate. With the subhumid climate of the BP and increased projected drying trends due to climate, this ecozone may be vulnerable to increased fires (Flannigan et al., 2005). Due to the hydrological

synergistic relationship between uplands and peatlands in this region (Petrone et al., 2015), regeneration following fire can have large implications for the water balance of both upland and peatland ecosystems. Thus, an improved under-standing of ecosystem dynamics following fires is needed.

Fire affects many aspects of the landscape, such as vegetation cover, soil characteristics, and nutrient availability, which subsequently affect the regeneration of new trees (Buck & St. Clair, 2012). Fire removes canopy cover and surface organic matter (OM) allowing for increased sunlight penetration and increased soil temperatures (Weber Stocks, 1998). Fire also impacts the availability of nutrients in the landscape through the immediate breakdown and mineralization of organic compounds, increasing the nutrient availability to regenerating plants (Dunn, DeBano, & Eberlein, 1979; Galang, Markewitz, & Morris, 2010; Hobbs & Schimel, 1984). Increases in inorganic N and P, how-ever, are often short lived through system recovery, leaching, erosion, wind, adsorption onto soil particles, and/or microbial and plant immobilization (Dunn et al., 1979; Hobbs & Schimel, 1984; Kishchuk et al., 2014; Wilbur & Christensen, 1983). Changes to the landscape follow-ing fire favour the regeneration of species suppressed under predisturbance conditions (Weber & Stocks, 1998). Indeed, fires often initiate the immediate succession of species that thrive in resource rich environments, such as trembling aspen (*Populus tremuloides* Michx). Although this potential exists, it can be affected by burn severity, which can vary spatially in Boreal forests. Recent studies in the BP of Alberta have linked burn severity to prefire conditions such as OM content, vegetation cover type and age, soil moisture, and hydrologic connectivity (Hokanson et al., 2015; Lukenbach, Devito, Kettridge, Petrone, & Waddington, 2015). However, such properties have yet to be linked to the recovery and migration of upland tree species.

Much of the current understanding of biogeochemical processes following fire in Boreal forests has been developed in upland forest soils, and fewer studies have been undertaken in peatland systems, which are found adjacent to forests in the BP. Fire has been shown to increase both N and P supply in temperate marsh systems and ombrotrophic bogs, although the magnitude of heightened availability is dependent on the time of burn and its severity (Wang et al., 2015; Wilbur & Christensen, 1983; Wu et al., 2012). Consistently, mineralization has been linked to zones having high organic N and P (Wang et al., 2015; Wilbur & Christensen, 1983; Wu et al., 2012), which suggests that if inorganic N and P supplies are greater in wetlands and riparian areas than in forests, these low-lying areas may be a significant source of nutrients postfire.

Indeed, some studies have observed increased export of TN, $Mg^{2+}$, $SO_4^{3-}$, $NO_3^-$, and TP into lakes following and are mobilized from sur-rounding wetlands and riparian areas rather than uplands (Burke, Prepas, & Pinder, 2005; Devito, Creed, & Fraser, 2005; Devito, Creed, Rothwell, & Prepas, 2000; Lamontagne, Carignan, D'Arcy, Prairie, & Paré, 2000; McEachern, Prepas, Gibson, & Dinsmore, 2000). Thus, due to the low occurrence of precipitation events with high enough intensity to generate preferential flow (along rooting channels) in upper soil layers, combined with deep water table depths and high storage capacity of forested soils, limits the generation of run-off from uplands into peatlands (Ferone & Devito, 2004; Redding & Devito, 2008; Redding & Devito, 2010). Because the storage capacities of wet-lands are less than in uplands, they are able to generate flow towards uplands and may therefore potentially transfer N and P between adja-cent land units (Devito, Creed, & Fraser, 2005; Devito, Creed, Gan, et al., 2005; Devito, Mendoza, & Qualizza, 2012; Ferone & Devito, 2004; Macrae, Devito, Creed, & Macdonald, 2006; Macrae, Redding, Creed, Bell, & Devito, 2005). Water transport, and possibly nutrient transport, can also occur through hydraulic redistribution. In moisture-limited areas, deep tree roots can tap into water

sources, such as groundwater and the water table and redistribute to drier soil depths (e.g., Dawson, 1993; Hultine et al., 2006). In other studies with resource-limited systems, broadleaf trees have been shown to extract nutrients and water from adjacent areas (e.g., Dawson, 1993). Thus, enhanced nutrients in wetlands postfire may result in enhanced nutrient supply to upland trees.

Although aspen seedlings have been recorded in drained riparian zones (Roy, Ruel, & Plamondon, 2000), it is uncertain if the presence of *P. tremuloides* in peatlands and peatland margins indicate areas where they may regenerate. Conversely, it is unknown if this observation can be linked to pre-existing roots in these areas that exploit resources, such as water and nutrients. The Utikuma Complex Wildfire of 2011 (SWF-060, ~90,000 ha, May 2011) can be used to understand if the lack of nutrient availability drove upland aspen regeneration into adjacent peatland margins, or further into peatlands, which has yet to be recorded in the literature.

The goal of this study was to determine if, and how aspen regeneration and succession in uplands, peat margins, and peatlands following fire correlates with physical conditions and nutrient availability across the landscape. This is done by addressing the following specific objectives: (a) to compare burned and unburned transects across peatland-upland gradients to characterize the individual and combined influences of fire and land unit position on soil and water nitrate ($NO_3^-$), ammonium ($NH_4^+$), and phosphorus (P) availability and potential aspen recovery postfire and (b) to relate aspen growth patterns with differences in soil conditions and nutrient availability across burned hillslopes, peatland margins, and peatlands. It is hypothesized that the presence and growth of aspen in peatlands are related to elevated N and P concentrations. It is also hypothesized that $NO_3^-$, $NH_4^+$, and P availability are greatest in burned peatlands and reduced in aspen uplands, which may cause the migration of trees into peatland margins during recovery.

## 2 METHODS

### 2.1 Study area

The Utikuma Research Study Area (URSA) is located in north central Alberta within the BP of Western Canada (56°6′N, 116°32′W; Depante, 2016; Devito et al., 2012). In May 2011, approximately 90,000 ha of URSA was affected by the Utikuma complex fire (SWF-060). The catchment area selected for this study was located on a coarse-textured outwash plain that contained a 39 ha pond char-acterized with a regional groundwater flow-through system (Lukenbach, Kettridge, Devito, Petrone, & Waddington, 2015; Smerdon, Devito, & Mendoza, 2005; Figure 1). The southwest portion of the lake was affected by the fire, which consumed upland canopies and adjacent peatlands that further experienced smouldering in hollows and margins (Hokanson et al., 2015; Lukenbach, Devito, et al., 2015). The nature of the crown fire sustained some peatlands and forested areas within the burned portion of the catchment. Trembling aspen (*Populus tremulodies Michx*.) dominated the overstory of burned and unburned uplands whereas spruce (*Picea* spp.) dominated peatland margins. Sampling locations within the peatland margins in the burned and unburned areas were selected based on their location along the peatland-forest gradient, and similarities in water table depth, ground water flow direction, and soil properties (Hokanson et al., 2015; Lukenbach et al., 2017). The depth of peat in peatland margins generally exceeded 0.15 m in unburned and burned areas; however, some margins in the disturbed areas were burned to the mineral soil layer (Hokanson et al., 2015; Lukenbach et al., 2017). Similarities in prefire vegetation communities also contributed to sample location selection; however, aspen seedlings and clones were observed in burned peatlands and peatland margin. Unburned peatlands and peatland mar-gins did not contain aspen (Depante, 2016).

Primary successional species in peat margins included *Polytrichum* mosses, common horsetail (*Equisetum arvense*), fire moss (*Ceratodon purpureus*), and willow (*Salix* spp.). Unburned sites and recovering peatlands contained *Sphagnum fuscum* and feathermoss in hummocks and hollows with Black spruce (*Picea mariana*) over-stories (Lukenbach, Devito, et al., 2015). We divided the landscape into four topography-based land units: (a) hilltops (top of aspen forests), (b) midslopes (middle of aspen hills), (c) peatland margins/ riparian zones, and (d) peatlands (including hummocks and hollow microtopography). Riparian zones/peat margins are classified as transition areas between uplands and forests that contain varying OM depths where the ground surface does not follow hummock-hollow microtopography (Dimitrov, Bhatti, & Grant, 2014; Hokanson et al., 2015). Six transects were sampled in this study, where three transects were located in the burned area and three in the unburned portion (Figure 1).

### 2.2 Soil physical properties and hydrology

Carbon to nitrogen ratios (C:N) for the July 2014 mineralization soils were prepared based on Land, Lang, and Barnes (1977) and Irwin, Curtis, and Coleman (1977), where dried samples were combusted by an elemental analyser (4010 Elemental Analyzer, Costech Instruments, Italy) coupled to a continuous flow isotope mass spectrometer (Delta Plus XL, Thermo-Finnigan, Germany) and yielded percent composition of carbon and nitrogen (University of Waterloo, Environmental Isotope Laboratory). Soil samples were also dried to calculate gravimetric water content, bulk density, and organic carbon content through loss on ignition (after Dean, 1974). The pH of remaining soil samples from the dis-tilled water extract (5:1 wet soil ratio) mineralization experiment was taken with a pH electrode.

To characterize the hydrological interaction between the peatland, margins, and hillslope, a monitoring network of wells was installed using 0.05 m diameter polyvinyl chloride following the method of Smerdon et al. (2005) adjacent to each study plot (Figure 1). Water levels and electrical conductivities in wells were measured weekly during the study periods using a temperature-level-conductivity meter (Solinst, Georgetown, Ontario, Canada). Weekly volumetric soil moisture content ($m^3/m^3$) was quantified with an ML2x Theta Probe (Delta-T, Cambridge) within the top 3 and 6 cm from the surface for every plant root simulator (PRS) probe location and recalculated to yield percent saturation.

### 2.3 Plant available nutrients and net mineralization rates

At each land unit, PRS™ probes (Western Ag. Innovations, Saskatoon) were deployed in both growing seasons to capture supply rates of anions and cations ($\mu g \cdot 10\ cm^2 \cdot month$). The probes were placed diagonally in the Litter Fall Horizon (LFH) layer in forested areas (0–3 cm burned; 0–10 cm unburned), and the top layer of peat in margins and peatlands (0–10 cm burned; and 0–10 cm unburned), which will be referred to as the "surface soil layer". Second sets of PRS probes were placed in the mineral soils of the forested area, along with riparian zone and peatland probes, approximately 10–20 cm from the surface. In some peat margins burnt close to mineral soil, the subsurface PRS probe was placed into mineral soil. The probes at depth will be referred to as the "subsurface soils," though it is important to note that they only capture approximately 20 cm of the rooting depth of recovering vegetation in the peatland and riparian zone. PRS probes were randomly placed in each hilltop, midslope, riparian zone, peatland hum-mock, and peatland hollow at the burned and unburned near surface (per land unit: $n$ = 18 burned, $n$ = 9 unburned all transects combined) and at the subsurface (per land unit: $n$ = 18 burned, $n$ = 9 unburned all transects combined; Figure 1). After 1 month of incubation, the probes were triple rinsed with distilled water

within 24 hr of collection (Western Ag Innovations Inc, 2010). Probes were then shipped to Western Ag. Innovations (Saskatoon, Saskatchewan), where they were washed with HCl and analysed colormetrically with a Technicon Autoanalyzer (Hangs, Greer, & Sulewski, 2004). Additional parameters were also quantified at each site during the removal and installation of PRS probes: Approximation of redox status (oxic, anoxic) was deter-mined using iron rods inserted to a depth of approximately 45 cm; depth to water table and ice, if present, were recorded manually, and the depth of the LFH or organics layer was recorded.

Net mineralization rates of N and P were measured along the same transects and locations as the PRS probes in 2014 ($n$ = 9 surface, $n$ = 9 subsurface per topographic position, Figure 1) using the buried bag technique (Eno, 1960; Hill & Devito, 1997). For each soil sample, a set of paired cores were taken, divided by minimum and maximum rooting zone depths, and placed in polyethylene bags. In the case of the peatland and riparian areas with greater than 20 cm of organics, minimum rooting zone cores were 0–10 cm and were taken from 10 to 20 cm depth. One core was placed into the soil layer from where it was retrieved, incubated, and removed after 4 weeks for extraction (Eno, 1960; Hill & Devito, 1997). The other bag was immediately extracted to determine $NO_3^-$, $NH_4^+$, and Soluble Reactive Phosphorus (SRP) availability at the time of the collection (Eno, 1960). Approximately 5 g of organic soil or 10 g of mineral soil were weighed into sterile cups, where 0.5 L of 2 M KCl was added to the sample to extract $NH_4^+$ and $NO_3^-$, and 0.5 L of distilled water was used for the determi-nation of water-extractable P (Hill & Devito, 1997). The samples were shaken for 2 hr, filtered with 0.45 μm Whatman filter paper, and kept cold (4 °C) until analysis. Soil extracts were run on a Bran-Luebbe Autoanalyzer III, (Seal Analytical) in the Biogeochemistry Lab at the University of Waterloo using standard colorimetric methods (Bran Luebbe AA3, Seal Analytical, Seattle, U.S.A., Methods G-102-93 [$NH_4^+$], G-109-94 [$NO_3^-$ + $NO_2^-$], G-103-93

[SRP]). To calculate net nitrification, net ammonification, and net P mineralization rates, the difference in concentration between the incubated soil sample and the initial soil sample were taken. Values greater than zero indicate net mineralization, and differences less than zero indicated net immo-bilization expressed as kg N or P/$m^3$ of dry soil (Hart, Nason, Myrold, & Perry, 1994).

### 2.4 Aspen growth patterns

A pair of aspen growth plots for each of the four land unit positions (total eight plots, 8 $m^2$ for each transects) were designated, and aspen were classified as small, medium, or large relative to the overall size distribution of *P. tremuloides* at the site. In both years, a subsample of aspen that represented those in each plot were taken where average stem height (m) and leaf area index (LAI) expressed in $m^2/m^2$ per plot area was calculated. LAI was measured destructively with a leaf area scanner (LI 3600, Li-Cor, Nebraska) at the end of both growing seasons (July through August in 2013 and 2014). The average LAI per size class (small, medium, large) per plot, was multiplied by the number of aspen per size class and summed for each plot. Aspen in plots located in for-ested areas were of sucker origin, seedlings dominated peatlands, and mixtures of seedlings and clones occupied peatland margins (Depante, 2016). Regenerating aspen were identified as clones if connections to surrounding and parent roots were observed, whereas seedlings contained individual rooting systems (Depante, 2016; DesRochers & Lieffers, 2001).

### 2.5 Statistical analysis

Tests showed that PRS probes, net N and P mineralization, and water chemistry data were non-normally distributed. As such, the Scheirer– Ray–Hare test, a non-parametric equivalent to the two-way analysis of variance (Dytham, 2011), was used to determine if there were effects of land unit position and fire on nutrient supply and mineralization rates. The Mann–Whitney *U* test was used to

further examine whether differences existed between soil layers and between years, whereas the Kruskal–Wallis test demonstrated the influence of topographic position on LAI and stem height. Further, average Spearman's rank-order correlations ($r_s$) illustrated the linkage between growth parameters and soil chemical and physical properties. All statistical analysis was performed on IBM SPSS Statistics version 20 (IBM Corporation).

## 3 RESULTS

### 3.1 Differences in soil physical properties with land unit position and disturbance

Soil/peat quality and biogeochemical conditions differed in the land-scape. Soil OM depths varied spatially and were dependent on both land unit position and disturbance ($p < .05$) (Table 1). Although OM depths were >0.15 m in both and did not differ between burned and unburned peatlands, the LFH layers were thinner in burned (0–0.03 m) than unburned upland forests (0–0.18 m). Undisturbed margins contained deep OM, whereas two of the three disturbed were burned to the mineral layer (see Lukenbach, Devito, et al., 2015, Hokanson et al., 2015, for more detail).

pH was greatest in forests and lowest in peatlands (Table 1). Fire senerally increased pH across all land units ($p < .05$); however, such increases were more prevalent in the margins and peatland than upslope and midslope areas (Table 1). Depths to anoxic conditions were greater in the forested areas and decreased into the peatlands areas in both years, and did not differ between burned and unburned areas (Table 1). Little temporal variability was observed in the depth of the oxic layer in forests over the study period, whereas the depth of the oxic layer in margins and peatlands became shallower over the incubation periods (data not shown). C:N ratios were greatest in peatlands and decreased into forests ($p < .05$ both depths), although there were no effects of fire ($p > .05$).

### 3.2 Differences in water table dynamics and soil moisture with land unit position and disturbance

Water table positions were lowest in burned and unburned forests, which exceeded 0.20 m from the surface and decreased with distance in peatlands (Table 1). Water table depths in burned and unburned hummocks did not significantly vary ($p > .05$), hollows fluctuated from 0.15–0.06 m (burned) and 0.15–0 m (unburned). Burned margins experienced the largest variability where the water table ranged 0.15 m below the surface to 0.07 m above. Unburned margins also experienced fluctuations with the WT initially at 0 m and decreasing to 0.15 m below the ground surface.

Soil saturation was lowest in forested areas and increased into riparian areas and peatlands in 2014, in burned and unburned sites ($p < .05$). With the exception of hummocks and hollows ($p < .05$), moisture content increased postfire ($p < .05$) across land units where upland soils showed the highest amount of saturation (Figure 2). This is likely due to the loss of surface OM, resulting in the lowering of the ground surface and proximity to the water table. Weak positive correlations also existed with rust measurements ($r_s = 0.34$, $p = .10$), where deeper water table depth yielded rust formation further from the surface.

### 3.3 Differences in nutrient supply and net mineralization rates with land unit position and disturbance

Nitrate-N supply rates were highly variable in margins and peatland hummocks compared with uplands (Figure 3a,b,d,e; Table 2). No effects of fire were observed ($p = .94$ and $p = .49$, in 2013 and 2014, respectively, all land units pooled). In general, supply rates did not vary between years and depths ($p > .05$). Net nitrification rates were positive and were greater and more variable in the margins and peatland areas at the surface, coinciding with the greater $NO_3^-$ supply rates (Figure

3b,c,e,f; Table 2). Rates, however, did not statistically vary- across land units where $p > .05$ (Figure 3c,f). Similar spatial trends in net nitrification and the lack of the effect of fire ($p > .05$) were also observed at depth.

Similar to what was observed for $NO_3^-$, $NH_4^+$ supply rates were generally greatest in peatlands and lowest in forests, and a significant difference across land units was found ($p < .05$). As was also found for $NO_3^-$, the impact of fire was not significant ($p > .05$) (Figure 4a,b, d,e; Table 2). Similar trends were observed at both depths. Spatial distributions and the lack of fire influence did not differ in 2014, although the ranges of $NH_4^+$ supply rates increased in unburned hollows with ranges of 0–60 μg N·10 $cm^2$·month. Similar to net nitrification rates, net ammonification rates did not change as a result of fire but were dependent on land unit position (Figure 4, Table 2). Furthermore $NH_4^+$ supply rates did not vary between individual burned and unburned land units ($p > .05$, Figure 4). The spatial patterns in net ammonification differed from net nitrification rates. In surface layers, net ammonification rates and extractable $NH_4^+$ pools (data not presented) were greatest in upland areas and lower in peatlands and mar-gins. These spatial patterns did not coincide with observed $NH_4^+$ supply rates (Figure 4a,b). In subsurface layers, net ammonification rates were low (approximately zero) across all land units and the effect of fire was negligible ($p > .05$).

Unlike $NO_3^-$ and $NH_4^+$, P supply rates were dependent on both land unit and fire (Figure 5a,b,d,e; Table 2). The patterns also differed between surface and subsurface soils. This was apparent in surface soils in 2013 (Figure 4a) where in burned margins and peatlands, P supply rate medians and ranges were significantly greater ($p < .05$) in hummocks (4.0–36.9 μg P·10 cm2·month) and hollows (2.2–171.1 μg P·10 cm2·month) and low in forests. In contrast, P supply rates were low in unburned areas and did not vary spatially ($p > .05$). P supply rates across land unit position in

surface soils during 2014 were consistent with those in 2013. In the subsurface, P supply rates in 2013 were similar between burned and unburned sections within the hillslopes and at riparian areas but were much lower at unburned sites in the peatland (Figure 5d). In 2014, P supply rates in the subsurface were similar to what was observed in the surface in 2014 and 2013.

Spatial patterns in net P mineralization rates in the surface were similar to what was observed for $NH_4^+$ trends, with elevated rates in upland areas relative to riparian areas and peatland (Figure 5c). Extract-able SRP pools followed mineralization rates in both layers. As was also observed for $NH_4^+$, the elevated net P mineralization rates were not reflected in elevated P supply rates in upland areas. Likewise, the elevated supply rates in the riparian and peatland areas did not reflect elevated net P mineralization rates. In the subsurface, net P mineralization rates were less spatially variable (Figure 5f).

### 3.4 Aspen regeneration in burned areas

Three seasons following the fire (August 2013), average aspen stem heights were greatest on recovering aspen hilltops and decreased into the margin and peatlands unit positions ($p < .05$; Table 3). However, during the fourth growing season following the fire (2014), stem heights in midslope and margins increased considerably, and there was no significant difference between stem heights in forests and mar-gins ($p = .40$). When all data were pooled, average aspen heights in 2014 exceeded 2013 ($p < .05$); however, post hoc analyses revealed that changes were statistically insignificant in most topographic positions with the exception of riparian zones ($p = .001$). The range of stem heights of aspen was greatest in peatlands although growth was the least (0.03 m) between years; conversely, average height of aspen in the margins increased by approximately 50%

(0.83 vs. 1.47 m) and contained suckers that grew up to 2.72 m. Likewise, an individual aspen in a peatland reached a height of 2.57 m.

Similar to stem heights, the leaf area of individual aspen was greatest in the forested areas (hilltops and midslope, $p = .13$) followed by low-lying areas (margins and peatlands, $p = .14$) in 2013 (Table 3). In 2014, aspen leaf area was smallest in the peatland, and there were no significant differences between recovering hilltops, midslopes, and margins ($p > .05$; Table 3), as was observed for stem heights.

With a few exceptions, nutrient supply rates were not related to aspen stem heights or leaf area ($p > .05$). Generally, growth parameters were significantly related to substrate quality (OM content; $p < .05$) where $r_s = -0.75$ and $r^2 = 0.57$ (stem height) and $r_s = -0.77$ and $r^2 = 0.59$ (leaf area). Significant negative correlations ($p < .05$) were observed with LFH depths when linked to LAI ($r_s = -0.39$, $r^2 = 0.15$) and growth ($r_s = -0.37$, $r^2 = 0.11$). Positive correlations were also observed between LAI and net ammonification rates ($r_s = 0.65$) and percent saturation ($r_s = 0.59$, $r^2 = 0.28$). Water table depth and stem heights were also significantly related where $r_s = 0.48$, $r^2 = 0.11$. Significant relationships ($p < .05$) existed between C:N ratios and net ammonification ($r_s = -0.69$ in both surface soils and at depth $r_s = -0.09$) and between C:N ratios and net nitrification ($r_s = -0.37$, in surface soils, $r_s = -0.05$ at depth).

## 4 DISCUSSION

### 4.1 Aspen growth patterns and relationships with nutrient dynamics

In general, net ammonification rates were positively correlated with aspen growth suggesting that the high quality of aspen litter (Lègarè, Paré, & Bergeron, 2015) enhances nutrient availability.

Although N transformations were greatest in recovering hilltops and midslopes, likely due to aspen litterfall, limited supply rates indicated immediate uptake further explaining high leaf area. Although C:N:P ratios of foliage were not measured in this study, Hemming and Lindroth (1999) and Desrochers, van den Driessche, and Thomas (2003) showed that fertilizers containing N did not greatly increase *P. tremuloides* growth further supporting that upland foliar N is sufficient to satisfy demand. This also shows that while $NH_4^+$ and P supply rates were high in peatlands, they were neither required nor beneficial for aspen regeneration. Therefore, growth in peatlands could be attributed to soil properties such as OM content and moisture.

### 4.2 Ecohydrology of aspen regeneration

The results in this study show that aspen stem height and LAI vary across topographic positions with the largest leaf area and tallest aspen in forests in 2013, but less variability across topographic positions in 2014. This is not surprising as aspen sucker growth rates exceed those of seedlings during the first few years after disturbance (Peterson & Peterson, 1992). In this study, suckers were the dominant form of regrowth in hilltops and midslopes (Depante, 2016). Further differences across the gradient can be linked to aspen suckers and their rooting zones in each land unit. Rooting systems are able to store energy for clone regeneration (Calder et al., 2011; DesRochers & Lieffers, 2001; Landhäusser, Silins, Lieffers, & Liu, 2003). Through wind dispersal postfire (Kay, 1993; Romme et al., 1997; Turner, Romme, Reed, & Tuskan, 2003), there was an increase in aspen seedlings in margins and peatlands indicating that seedlings do not have the connectivity and resource stores for large leaf areas (Landhäusser et al., 2003) unlike aspen in forested areas.

Multiple studies have shown that aspen re-establish better on mineral soils (Johnstone & Chapin III, 2006; Kay, 1993; Lafleur, Cazal, Leduc, Bergeron, 2015), whereas the burned peatlands in this

study had OM content exceeding 85% at the surface (data not presented). This corroborates the additional correlations where growth was greatest when the water table was furthest away from the surface as evidenced by rust measurements. Likewise, seedling germination has been found to be best when in moist mineral soil (Wolken, Landhäusser, Lieffers, & Dyck, 2010), such as forests in this study that were ~75% saturated. This dem-onstrates that while the water table was metres from the surface in uplands (Hokanson et al., 2015), hydraulic redistribution likely occurred to meet water, moisture, and oxygen demands (Brown et al., 2010; Depante, 2016; Lazerjan, 2014; Petrone et al., 2015). Conversely, anoxic soils with high OM such as peat have been found to reduce plant turgor and initiate wilting as a result of oxygen deficiencies in roots (Bradford & Hsiao, 1982; Landhäusser et al., 2003). Aspen growth and LAI were greatest when the depth to the water table and rust were furthest away from the surface indicating that despite the BP's subhumid climate, soil moisture in forests is sufficient to sustain aspen regeneration.

Notably, high mineral content and lowered depth to water table and moisture between years at margins relative to peatlands suggests that margins could be more favourable for regeneration and growth as indicated by increased stem heights and LAI. Water table fluctuations in peat margins may have increased the amount of oxygen available to rooting zones (Landhäusser et al., 2003), lowering anoxia and resulting in heightened growth in 2014. Thus, additional soil physical properties, such as OM, litter quality, and moisture may have a larger influence on aspen growth and regeneration postfire. Although nutrients were abundant in peatlands, especially hollows where most aspen were found (Depante, 2016), excess nutrients may not be the largest and only factor that drove aspen recovery in adjacent uplands. Instead, roots found in margins and peatlands originating in forests may have a large role in transporting water across land units.

### 4.3 The role of fire and land units on soil nutrients

Results here are similar to the findings of Macrae et al. (2006) where $NO_3^-$ and $NH_4^+$ concentrations were greatest in low-lying areas, and nutrient availability varied spatially across a landscape irrespective of disturbance. Thus, the findings in this study reject the hypothesis that soil $NO_3^-$ and $NH_4^+$ availability are governed largely by site scale properties and processes (soil moisture, anoxia, organics) and less by fire.

Nitrate may have returned to a state of limited availability as seen in prefire conditions and may be attributed to changes in resource availability during early succession. Along with OM in margins and peatlands (Macrae et al., 2006; Wilbur & Christensen, 1983), elevated $NO_3^-$ supply rates in burned and unburned margins were observed during both incubation periods. This may suggest the presence of nitrate hotspots in the BP where evidence is reflected in changes of rust depths suggesting that water table fluctuations lead to soil aeration, and the lower $NH_4^+$ suggest subsequent oxidation to $NO_3^-$ and nitrification (Hill, 1996; Vidon et al., 2010). Along with precipitation approaching evapotranspiration in 2013 and 2014, the loss of OM in burned margins resulted in the lowering of the ground surface and water table distance, thus reducing nitrate supply rates and nitrification relative to unburned sites. Furthermore, the translocation of $NH_4^+$ into burned mineral soils and elevated pH could support nitrification and $NO_3^-$ transformations (Prieto-Fernández, Acea, & Carballas, 2012; Ste-Marie & Paré, 1999; Simard, Fyles, Paré, & Nguyen, 2001; Shenoy, Kielland, & Johnstone, 2013). Conversely, a reduction of nitrate in forested stands can be attributed to its uptake kinetics in aspen as $NO_3^-$ is the preferred form of inorganic N for root suckers (DesRochers & Lieffers, 2001; Min, Siddiqi, Guy, Glass, & Kronzucker, 1998), which explains the rapid regeneration in uplands dominated by aspen clones. Therefore, while soil $NO_3^-$ likely returned to its limited availability similar to prefire conditions in forests, margins might be favourable areas

for aspen regeneration and nitrate production should declining water table levels and soil moisture continue.

Similar to nitrate, the lack of an effect of fire could indicate the return of ammonium to predisturbance levels. The spatial variability could be attributed to the vegetation composition of each land unit whereby $NH_4^+$ demand of recovering forests may have exceeded those of low-lying areas (Fritz, Lamers, Riaz, van den Berg, & Elzenga, 2014; Macrae et al., 2006). Furthermore, the incomplete burning of OM likely resulted in high N mineralization (Certini, 2005; Wilbur & Christensen, 1983), and this is the first study to observe this in BP peatlands. Continuously, waterlogged and anoxic soils may have fur-ther allowed $NH_4^+$ build-up in peatlands and the inhibition of ammonium oxidation (Macrae et al., 2006), which is corroborated by small changes in rust depth as the water table in peatlands remained close to the surface. Further, acidic hummocks and hollows as seen in this study and others in Western Canada (Bayley, Thormann, & Szumigalski, 2005) often inhibit nitrification and not ammonification (Dancer, Peterson, & Chesters, 1973). Net ammonification rates were also dependent on land unit, though $NH_4^+$ turnover was instead highest in forests and may be attributed to N-rich aspen litter and low C:N ratios favouring decomposition (Lègarè et al., 2015). Thus, differences across land units may be attributed to the substrate quality but may not have been detected in the supply rates because of regeneration in aspen uplands. Importantly, recovering vegetation may be dependent on their own litter to satisfy $NH_4^+$ demands and may not need additional ammonium from peatlands or margins that may other-wise be transported by rooting zones.

Landscape position and the effect of fire appeared to have an effect on soil P. In the surface layer and maximum root zone depth in 2013, P supply rates in the unburned sites did not vary spatially,

whereas the burned site showed increases into the peatland. Losses of the LFH layer may have destroyed plant available P in forests, whereas the mineralization of high organic P may explain peatlands trends. Wang et al. (2015) showed that differences in P fractions varied with temperature as increased temperatures led to increased P mobility. Therefore, the fire in peatlands likely mineralized high amounts of P, where temperatures may have been below those required for P volatilization. Different microforms may also explain differences in plant available P. A recent study by Lukenbach, Hokanson, et al. (2015) at URSA found that water repellency varies with burn severity, vegetation type, and microform. For example, wettability was lowered in *S. fuscum* hummocks when burn severity was high, with similar findings in feathermoss hollows that experienced low severity burns (Kettridge et al., 2015; Lukenbach, Hokanson, et al., 2015). Because most of the microforms in this study were severely burned, increased wettability, lowered distance to the WT, and anoxia in hydrophobic hollows may explain high P supply rates compared with hummocks.

P supply rates during recovery can also be attributed to differences in vegetation demand and uptake requirements across land units. Prolonged P in peatlands postfire may be explained through high mineralization of large P bound in OM, thus exceeding required amounts of orthophosphates for regenerating bog species (Hauer & Spencer, 1998). Similarly, P only becomes the limiting nutrient in *Sphagnum* when in excess N, which is supported by colimitations of N on P in *Sphagnum* (Aerts, Wallen, & Malme, 1992; Kellogg & Bridgham, 2003; Kielland, 2001; Phuyal, Artz, Sheppard, Leith, & Johnson, 2007), though *Sphagnum* demand for phosphorus has yet to be investigated in the literature. Relationships between iron (Fe) and manganese (Mn) may also play a role in the high amounts of P in peatlands. Furthermore, the redox conditions of the waterlogged soils may have allowed the release of P bound to Fe through the transformation of $Fe^{3+}$ to soluble

$Fe^{2+}$ along with the reduction of $Mn^{5+}$ to $Mn^{4+}$ (Chambers & Pederson, 2006). Increases of Fe and Mn in peatlands (data not presented) may have indicated that anaerobic soils released plant available P (Maynard, O'Geen, & Dahlgren, 2011; Venterink, Davidsson, Kiehl, & Leonardson, 2002). Similar to $NH_4^+$, P supply rates in forests may have been limited by binding to Fe, Mn, and Ca in mineral soils, along with regenerating aspen uptake (Macrae et al., 2005), despite high net SRP mineralization rates at the surface. Although P supply rates were limited in forests likely due to Ca, Mn, or Fe binding, net P mineralization rates showed high P turnover and likely immediate uptake by aspen (Macrae et al., 2005). Although the interaction between fire and land unit was observed in 2013, soils at depth in 2014 showed that only fire explained elevated P supply rates. Although foliar nutrients of aspen were not taken, Penna et al. (2012) found that PK and N additions correlated with increased foliar P in reclaimed soils, which may explain limited supply rates in forests. Therefore, because P medians did not vary across land units, P supply rates may be returning to prefire levels.

Unlike $NO_3^-$ and $NH_4^+$ where supply rates and concentrations likely returned to prefire rates, the effect of fire disturbance and land unit was evident with P availability. Results in this study show that dif-ferences in soil characteristics after fire, such as OM content, moisture, water table position, anoxia, soil properties (e.g., hydrophobicity) and vegetation demand may explain varying trends across forests and peatlands (Kellogg & Bridgham, 2003). Importantly, these mineralization and supply rates show that nutrient-rich aspen litter in uplands and hilltops act as their own sources for nutrients (Huang & Schoenau, 1998). Similar to N, aspen likely do not rely on additional areas or sources, such as peat, to satisfy P requirements.

### 4.4 Water chemistry

$NO_3^-$, $NH_4^+$, and SRP in subsurface water varied across land units within burned and unburned areas. Although it is possible that these nutrients were elevated immediately after disturbance (McEachern et al., 2000), they could have been flushed into adjacent hilltops and midslopes, though was also observed in unaffected areas (Macrae et al., 2005). Although forested areas generally contained higher $NO_3^-$ and $NH_4^+$ relative to lowlands, it is unlikely that aspen depended on deep-water sources for nutrients, further supporting that aspen litter act as a significant source for N and P.

### 4.5 Implications for BP succession

Although the detection of aspen in saturated areas has been observed postdisturbance (Kay, 1993; Roy et al., 2000), this is the first study to report aspen in peatlands postfire. Along with wind dispersion, the deposition of mineral material and access to water may have allowed favourable conditions for early aspen establishment (Latva-Karjanmaa, Suvanto, Leinonen, & Rita, 2003). This was especially evident at peat margins where aspen growth exceeded those found in peatlands between years.

Although aspen seedlings typically grow at a slower rate than suckers (Peterson & Peterson, 1992), excess P as a result of anoxia and fire suggests that aspen uptake was low and growth was limited as reflected in stem height and leaf area. Thus, although nutrients are limited in uplands, the recycling of their high quality litter is sufficient during regeneration, and additional sources from other areas such as peatlands are not needed. Aspen regeneration in peatlands cannot be attributed to nutrient availability alone, but additional controls such as soil moisture must also be considered together (Hemming & Lindroth, 1999).

If seedlings continue to thrive, stand replacement of coniferous species, such as black spruce, to aspen can occur after severe fires (Johnstone & Kasischke, 2005), though it is uncertain if this could occur in peatlands given differences in OM content and nutrients. However, the suckering rooting system of aspen and its role in hydraulic redistribution (Lazerjan, 2014; Petrone et al., 2015) could aid in the potential shifts of succession patterns in peatlands and margins. A pos-sible mechanism for this may be through the uptake of peat and riparian zone water that is subsequently redistributed (Depante, 2016; Lazerjan, 2014) and transport into surrounding hillslopes. This may dry out peat margins in the already subhumid climate. Although net nitrification and $NO_3^-$ fluxes were not correlated with growth, abundant $NO_3^-$ in margins, as found in this study, may stimulate root suckering there. The exposure of mineral soils at margins (or low OM content) and decreased distance to the water table could further favour aspen regeneration thus preventing peat formation. Therefore, the role of aspen in peatland margins must be further investigated to understand their potential influence on recovery and the conditions needed to transform areas where they are not usually found.

## 5 CO NC LUSIO N

This study has shown that nutrients and aspen distribution and growth vary across recovering topographic land units. With the exception of net ammonification, relationships between nutrient availability and *P. tremulodies* did not exist. Due to the immediate regeneration of primary succession species, such as aspen, $NO_3^-$, and $NH_4^+$ likely returned to prefire levels. Conversely, *P. tremuloides* existence in burned peatlands was not explained by elevated P supply rates. This suggests that additional sources N and P were not required for re- establishment and that forest litter was sufficient for regeneration. Although aspen seeds were likely blown into the surface layer of

burned peat, this research showed that high OM, anoxia, and water-logged soil might have inhibited further growth into burned peatlands. Conversely, mineral soils (low OM) along with lowered water table positions favoured regeneration in peatland margins. When consider-ing the fate of land units and aspen in the BP, future studies must con-sider soil physical properties and nutrient status, along with the interactions between aspen roots and peat margins. Such long-term ecohydrological monitoring would help in predicting the trajectories of forests and the potential losses of peat margins with increased disturbances.

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**TABLE 1** Median aspen stem heights (m) and aspen leaf area index for off eight study plots per land unit position in August 2013 and 2014 (third and fourth growing season following the fire disturbance)

| Depth | Land unit | Burn/unburn | LFH depth (cm) | Depth to water table (cm) | Rust depth (m) | OM % | C:N | pH |
|---|---|---|---|---|---|---|---|---|
| Surface | Hilltop | Burn | 0.04 (0.01–0.06) | >−0.15 | 0.65(3–65) | 46 (37–84) | 28 (27–32) | 6.5 (5.6–7.0) |
| Surface | Hilltop | Unburn | 0.10 (0.04–0.15) | >−0.15 | 0.65(1–65) | 72 (37–88) | 27 (24–45) | 6.2 (5.4–6.6) |
| Surface | Midslope | Burn | 0.05 (0.01–0.18) | >−0.15 | 0.29(2.5–65) | 45 (26–88) | 25 (26–41) | 6.6 (5.5–7.0) |
| Surface | Midsole | Unburn | 0.08 (0.04–0.19) | >−0.15 | 0.24(0.05–0.65) | 78 (37–91) | 27 (25–31) | 6.4 (5.8–6.8) |
| Surface | Margin | Burn | 0.15 (0.01–0.20) | −0.06 (−0.15 to 0.07) | 0.0(1–0.65) | 79 (35–87) | 23 (19–29) | 6.9 (5.5–7.6) |
| Surface | Margin | Unburn | >0.20 | −0.15 (−0.15 to 0) | 0.13(0.01–0.65) | 88 (80–91) | 26 (2–52) | 5.3 (4.9–6.0) |
| Surface | Hummock | Burn | >0.20 | −0.13 (−0.15 to 0) | 0(0.02–0.65) | 96 (85–98) | 66 (44–91) | 3.7 (3.4–7.1) |
| Surface | Hummock | Unburn | >0.20 | >−0.15 | 0.26(0.55–0.65) | 98 (91–102) | 78 (48–111) | 3.7 (3.5–4.0) |
| Surface | Hollow | Burn | > − 0.20 (0.01–0.20) | −0.06 (−0.15 to 0.06) | 0.15(0.02–0.65) | 86 (33–119) | 30 (14–42) | 6.5 (3.7–7.0) |
| Surface | Hollow | Unburn | >0.20 | −0.15 (−0.015 to 0) | — | 94 (87–98) | 49 (37–77) | 4.3 (3.5–6.8) |
| Subsurface | Hilltop | Burn | — | — | — | 4 (3–5) | 25 (20–47) | 5.3 (5.0–6.5) |
| Subsurface | Hilltop | Unburn | — | — | — | 4 (2–38) | 18 (10–26) | 6.1 (4.8–6.4) |
| Subsurface | Midslope | Burn | — | — | — | 8 (1–79) | 23 (22–32) | 5.3 (4.9–6.6) |
| Subsurface | Midslope | Unburn | — | — | — | 2 (2–69) | 19 (13–26) | 5.5 (5.0–6.0) |
| Subsurface | Margin | Burn | — | — | — | 83 (5–93) | 21 (19–26) | 6.9 (6.2–7.6) |
| Subsurface | Margin | Unburn | — | — | — | 89 (28–94) | 24 (19–37) | 5.5 (4.4–6.4) |
| Subsurface | Hummock | Burn | — | — | — | 95 (85–102) | 42 (31–77) | 5.4 (3.8–6.1) |
| Subsurface | Hummock | Unburn | — | — | — | 94 (80–100) | 46 (23–75) | 4.2 (3.9–6.4) |
| Subsurface | Hollow | Burn | — | — | — | 88 (18–97) | 30 (15–72 | 6.1 (3.4–7.1) |
| Subsurface | Hollow | Unburn | — | — | — | 94 (85–97) | 53 (17–64) | 5.1 (3.7–6.5) |

**TABLE 2** Median LFH depth (cm), depth to water table (cm), rust depth (cm), pH, C:N, and OM % values for 2014 surface and subsurface soil

| Depth | Year | Interaction | $N–NO_3^-$ | Nitrification | $N–NH_4^+$ | Ammonification | P | SRP mineralization |
|---|---|---|---|---|---|---|---|---|
| Surface | Johnstone | Disturbance | 0.97 | — | 0.49 | — | <0.05* | — |
| | Johnstone | Land unit | 0.06** | — | <0.05* | — | 0.25 | — |
| | Johnstone | Disturbance x land unit | 0.23 | — | 0.42 | — | <0.05* | — |
| Surface | 2014 | Disturbance | 0.53 | 0.31 | 0.02* | 0.26 | <0.05* | 0.13 |
| | | Land unit | 0.17 | 0.57 | 0.01* | <0.05* | 0.4 | <0.05* |
| | | Disturbance x land unit | 0.77 | 0.38 | 0.94 | 0.47 | 0.15 | 0.74 |
| Subsurface | 2013 | Disturbance | 0.69 | — | 0.81 | — | <0.05* | — |
| | | Land unit | 0.06** | — | <0.05* | — | 0.76 | — |
| | | Disturbance x land unit | 0.56 | — | 0.48 | — | <0.05* | — |
| Subsurface | 2014 | Disturbance | 0.60 | 0.17 | 0.27 | 0.39 | <0.05* | 0.19 |
| | | Land unit | 0.01* | <0.05* | 0.06* | <0.05* | 0.39 | 0.91 |
| | | Disturbance x land unit | 0.54 | 0.73 | 0.70 | 0.43 | 0.14 | 0.28 |

**TABLE 3** The *p* values from Scheirer–Ray–Hare tests indicating if significant interactions exist between disturbance and land unit with $N–NO_3^-$ supply rates, net nitrification rate, $N–NH_4^+$ supply rates, net ammonification rate, P supply rates, and SRP mineralization

| Land unit | Year | Stem height (m) | | LAI ($m^2/m^2$) | |
|---|---|---|---|---|---|
| Hilltop | 2013 | 1.23 | (0.55–2.15)[a] | 0.16 | (0.13–0.19)[a] |
| Midslope | 2013 | 1.20 | (0.36–2.52)[a] | 0.30 | (0.20–0.57)[ab] |
| Margin | 2013 | 0.83 | (0.20–2.17)[bc] | 0.14 | (0.02–0.61)[ab] |
| Peatland | 2013 | 0.74 | (0.26–1.84)[bd] | 0.04 | (0.02–0.13)[c] |
| Hilltop | 2014 | 1.28 | (0.82–2.10)[a] | 0.46 | (0.23–0.46)[b] |
| Midslope | 2014 | 1.40 | (0.78–2.38)[a] | 0.47 | (0.13–0.99)[ab] |
| Margin | 2014 | 1.47 | (0.74–2.72)[bd] | 0.14 | (0.02–0.76)[ab] |
| Peatland | 2014 | 0.77 | (0.47–2.57)[d] | 0.06 | (0.04–0.15)[c] |

*Note*. LAI = leaf area index. Supercript indicate data that are significantly correlated.

*Data indicate significant interactions when $p < .1$.

**Data indicate strong significant interactions when $p < .05$.

***Data are very strong $p < .01$.

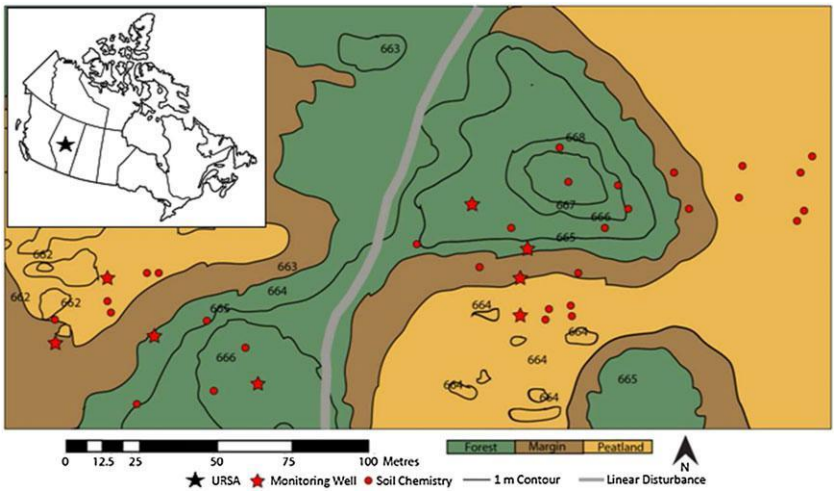


**FIGURE 1** Soil chemistry and monitoring well locations for the burned portion of the study catchment in each land unit position

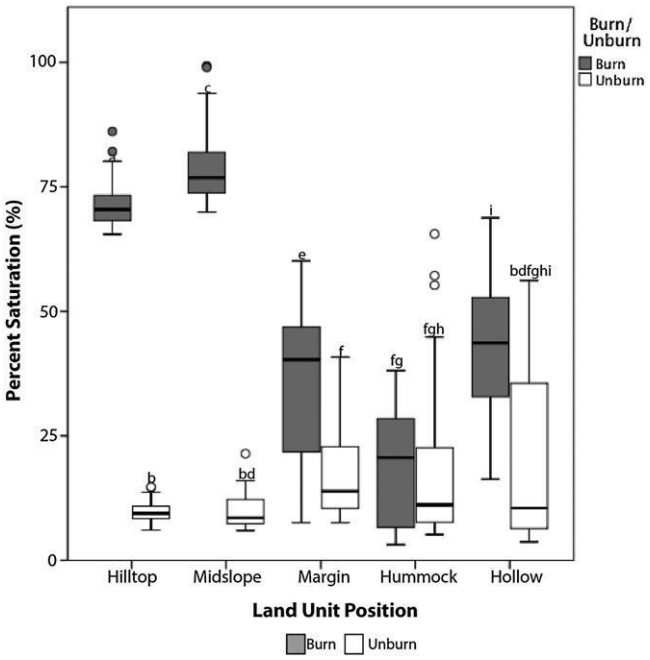


**FIGURE 2** Soil moisture expressed as percent saturation of plant root simulator probe locations of aspen vegetation plots and reference transects across land unit positions in 2014. Letters annotate statistical differences ($\alpha = .05$)

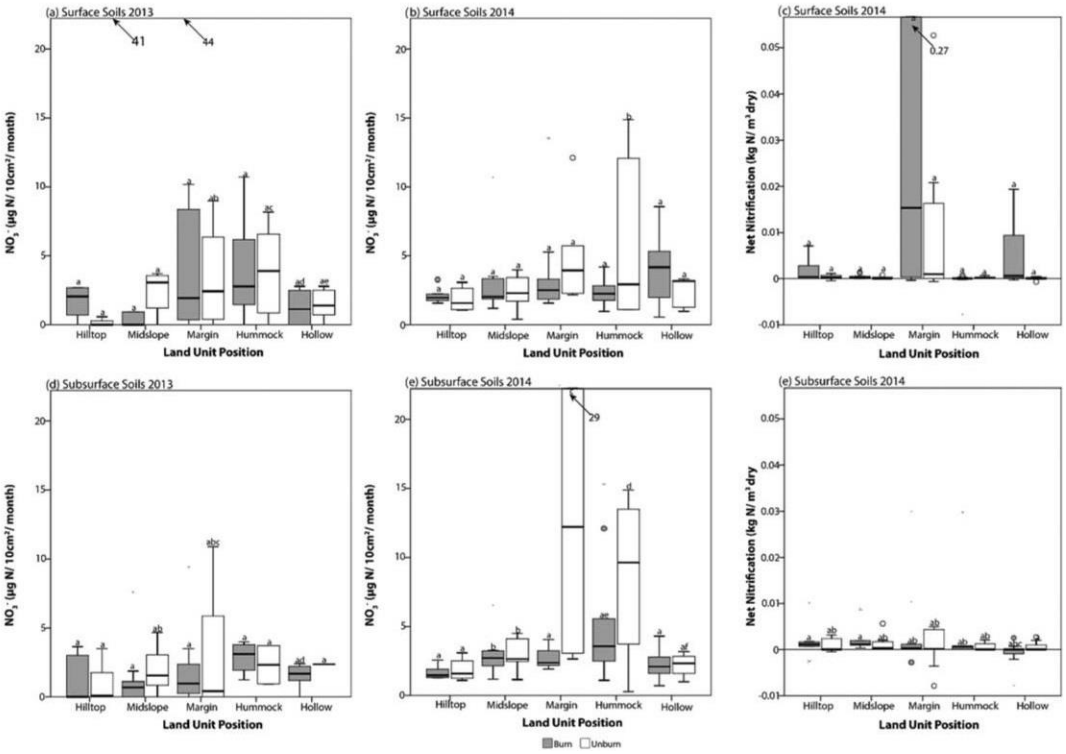


**FIGURE 3** $N–NO_3^-$ supply rates for surface soils (a,b) and subsurface soils (d,e) in aspen vegetation plots and reference transects of different land unit positions during 2013 and 2014, respectively; *n* = 18 burn and 9 for unburned (see Figure 1). Net nitrification rates for the surface (c) and at depth (d) are also displayed. Circles are values 1.5 times the interquartile range from the median, and asterisks are values 3.5 interquartile range from the median. Letters annotate statistical differences (α = .05)

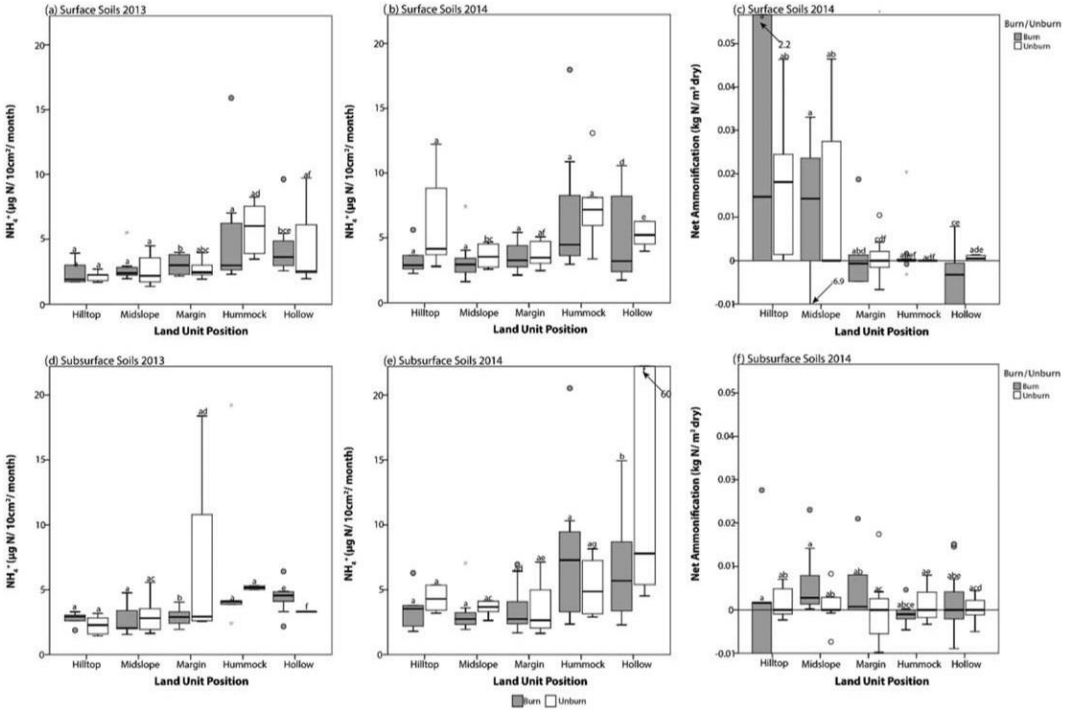


**FIGURE 4** $N–NH_4^+$ supply rates for surface soils (a,b) and subsurface soils (d,e) in aspen vegetation plots and reference transects of different land unit positions during 2013 and 2014, respectively; *n* = 18 burn and 9 for unburned (see Figure 1). Net ammonification rates for the surface (c) and at depth (d) are also displayed. Circles are values 1.5 times the interquartile range from the median, and asterisks are values 3.5 interquartile range from the median. Letters annotate statistical differences (α = .05)

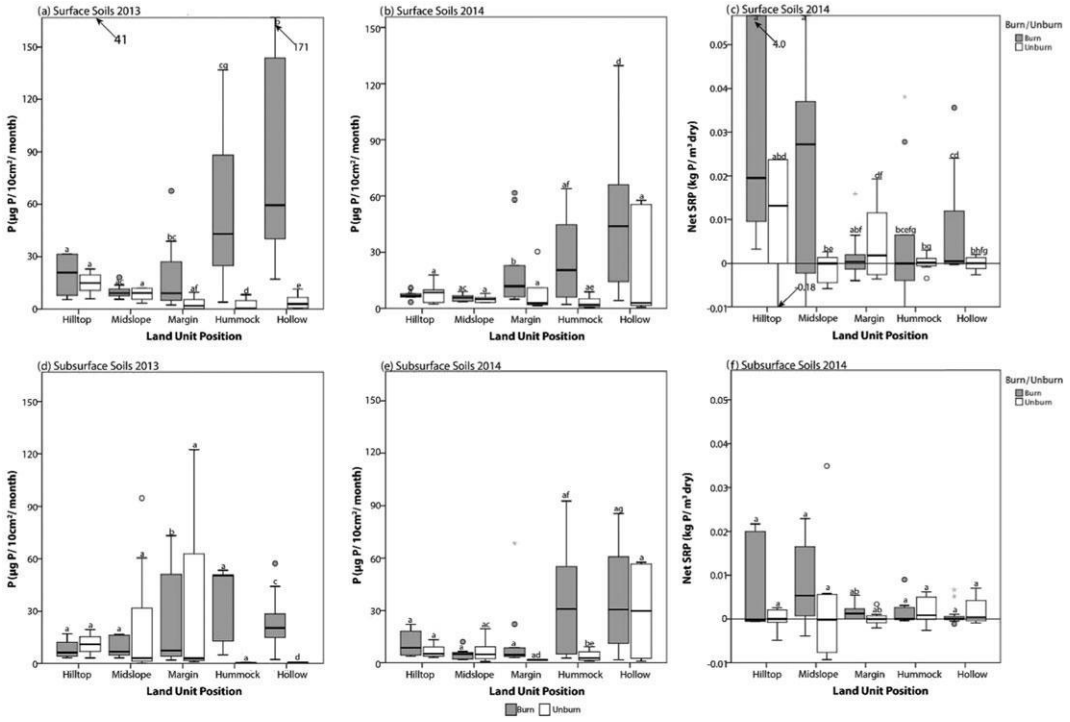


**FIGURE 5** P supply rates for surface soils (a,b) and subsurface soils (d,e) in aspen vegetation plots and reference transects of different land unit positions during 2013 and 2014, respectively; $n$ = 18 burn and 9 for unburned (see also Figure 1). Net ammonification rates for the surface (c) and at depth (d) are also displayed. Circles are values 1.5 times the interquartile range from the median, and asterisks are values 3.5 interquartile range from the median. Letters annotate statistical differences ($\alpha$ = .05)